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Research Article

Radiation of the microcaddisfly genus *Orthotrichia* (Trichoptera, Hydroptilidae) in Australia*

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Abstract

Orthotrichia is the most species rich of the hydroptilid genera found in Australia, and is postulated to be a relatively recent arrival from the Oriental Region. The genus has an almost worldwide but patchy distribution, represented by close to 280 species among which the Australian fauna of 55 species represents around 20%. In an attempt to understand the radiation of the genus in Australia, this paper explores the morphology and biology of Australian species and discusses a number of contrasts with reports on the biology of congeners in the Northern Hemisphere. The possible significance of these differences in Australian representatives of the genus is suggested to have played a role in the 'success' of the genus in the region. The value of life history studies to our understanding of biodiversity and biogeography is emphasized.

Key Words

Hypermetamorphosis, larvae, life history, pupae

Introduction

Among Australian Trichoptera, the family Hydroptilidae is the second largest family in terms of species richness, numbering some 158 described species. Currently, these are referred to 15 genera. In a conference paper presented in 2015, Wells and Johanson (2016) discussed possible origins of the Australian hydroptilid fauna, postulating Oriental origins for many taxa, and Gondwanan affinities for others. One of the genera suggested to have Oriental origins is the genus *Orthotrichia* Eaton, 1873. Such taxa are thought to have arrived in Australia when the continent moved to close proximity with the Eurasian plate some 5.3 to 1.6 mya, probably before the land bridge between New Guinea and Australia was completely disrupted around 10,000 years ago.

When Marshall (1979) reviewed the genus *Orthotrichia* she noted that no members of the genus were known from "… Central or South America or the Australian region". Even today only six species of *Orthotrichia* are known from the Neotropical Region (Harris and Davenport 1999; Harris and Rasmussen 2019; Morse 2022). In contrast, Australia's 55 species represent about 20% of the world *Orthotrichia* species. Furthermore, with around 27 species described from New Guinea (three of which are also recorded from northern Australia), and one species from Vanuatu, the fauna of the Australian Region represents close to 30% of the world's *Orthotrichia* fauna of just over 270 species (Morse 2022). The genus is also rich in species in sub-Saharan Africa (Wells and de Moor 2020).

Marshall (1979) described *Orthotrichia* as a highly specialized and very successful genus and commented that it "… is the only hydroptilid genus which has a truly tropical component …". Although probably other similar genera are now known, the thesis of a "truly tropical component" is supported by the currently known distribution of species

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in the Australian Region, namely the rich New Guinea fauna and the fact that a majority of Australia's species are described from the warmer and wetter northeast of the continent (Cartwright et al. 2013, unpublished conference report); no *Orthotrichia* species have been recorded from the southwest and only one species is known from Tasmania.

The Australian fauna

What has made this genus so successful, in the sense of species richness, especially in the warmer, wetter northern regions of Australia (and in New Guinea)? Is it just the richness of suitable habitats? Immature stages of Australian *Orthotrichia* species are generally found in streams with moderate to swift flow over rocky substrates. This contrasts with the (putatively) slow-flowing streams or lentic habitats from which Northern Hemisphere species were reported by Ross (1944—North America) and Nielsen (1948—northern Europe), habitats also attributed to the genus by Wiggins (1977, 2004) and Marshall (1979) and recently recorded by Harris and Rassmussen (2019—Florida). In comparison with the abundance of Australian species, such as some *Hellyethira* and *Oxyethira* species, that are often abundant in light collections, most collections of adults of Australian *Orthotrichia* species have been small—generally few specimens of any species are collected at any one time, generally taken only at lights or in small Diptera-type suction traps; rarely have they been collected using a sweep net, or Malaise trap. Most Australian species are known from few sites, some from only the type locality. Only a few northern Australian species have been collected as adults beside still-water bodies (billabongs) and sometimes these have been taken in quite large numbers. With much searching a few larvae of two species have been found in these lentic systems (Wells 1991).

Larvae

Larvae of *Orthotrichia* are distinctive among hydroptilids. Most notable in all instars is the labrum which bears a median tooth-like structure (Fig. 1). Other diagnostic features in the final instar larvae are the arrangement of four apotomes on the ventral head and short setae on the body. As is the situation for most hydroptilids, the larvae pass through four short, free-living instars. They then undergo a hypermetamorphosis: the fifth (final) instar develops a quite different shape, the abdomen swelling disproportionately. Following the moult to final instar, the larva begins to build a case that is characteristic for *Orthotrichia*, a "wheat-seed"- or "caraway seed"-shaped case built of silk secretion alone, usually strongly chitinised with the surface sometimes exhibiting distinctive sculpture (Figs 2–5, 10, 11, 13; see Wells 2020). In the early instars, *Orthotrichia* larvae usually resemble those of *Hydroptila* (Nielsen 1948; Marshall 1979), having short legs, short body setae and three caudal tracheal gills that are assumed to serve a respiratory function (Fig. 9; see Nielsen 1948: 166). The final instar larvae, unlike those of hydroptiline genera, are somewhat dorso-ventrally flattened and have the legs short and sub-equal in length (Figs 7, 8). Few larvae of Australian species have been identified to species.

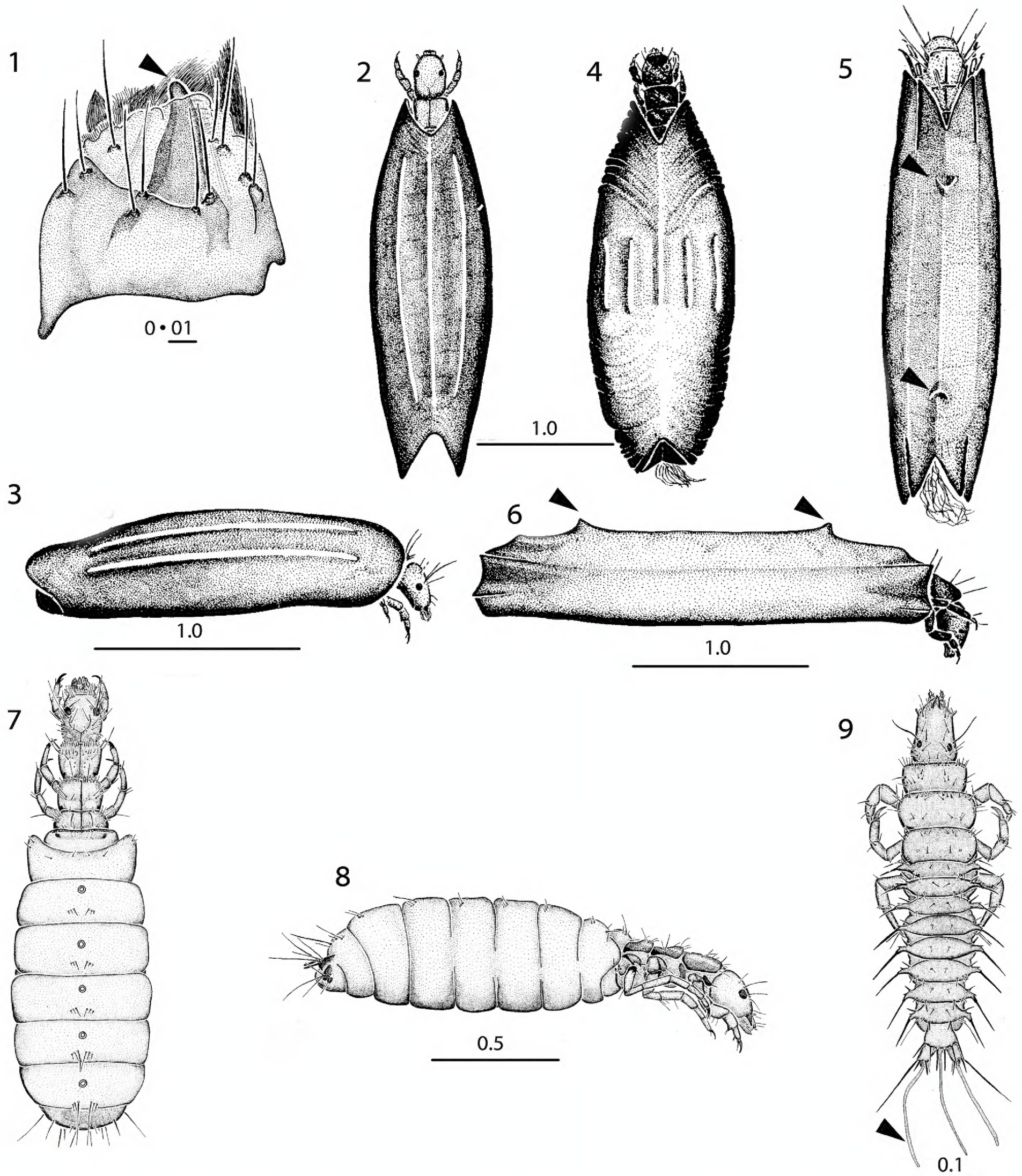
Late final instar larvae and pupae of *Orthotrichia* fit tightly into their often heavily chitinised cases (Figs 10–13) and the pupae are usually difficult to remove. The pupal cases can often be found in rock crevices and other irregularities on rock surfaces, sometimes on the upper surface, but usually beneath stones; sometimes a few pupae are found nested together. Cases are difficult to dislodge, being tightly attached. With the exception of a group discussed below, most pupae appear to exhibit no features atypical of hydroptilids in general.

Adults

In general appearance, adults of *Orthotrichia* resemble those of *Hydroptila*: the wings are usually patterned a mottled brown/grey and pale cream-white although in some species the vestiture is dark grey to black. The antennae are usually long, in males comprising 23–32 segments, around 20–26 in females, and have two or more dark coloured bands of flagellomeres; the flagellomeres of males usually bear numerous placoid sensilla (Wells 1984: plate X(a)). Most adults are quite small with the forewing length around 2 to 3 mm, although some members of the Australasian *aberrans*-group have forewing lengths of 4 to 5 mm. In other respects, *Orthotrichia* species conform to the general arrangement for hydroptilids, except that males often exhibit considerable modification of genitalic structures, providing a rich source of autapomorphies for separation of morphospecies and for study (Figs 18, 20, 22, 24–26, 28–33). Females usually can be assigned readily to the genus *Orthotrichia*, and the few that have been paired with males exhibit some clearly diagnostic features (Figs 19, 21, 23, 27).

Males of many Australasian species have quite a prominent lobe on the ventral abdomen, bearing a brush of blunt black setae (Figs 18, 20, 22, 24, 25). This lobe varies in position: generally, it is situated on abdominal segment VII but in some species occurs on VIII or IX. Among males of Australasian *Orthotrichia* other variable features are sometimes associated with segments VIII–X: dorsally one or two pairs of long, black, generally stout, socketed spines may be present either medially or on the distal margin of VIII (Figs 26, 29, 31, 33); spiny processes may be associated with segment IX, lying above tergite X, dorsally or laterally (Figs 26, 29, 31)—some of these arise from deep, asymmetric ventral apodemes; and spines or other forms of sculpturing may be present on tergite X.

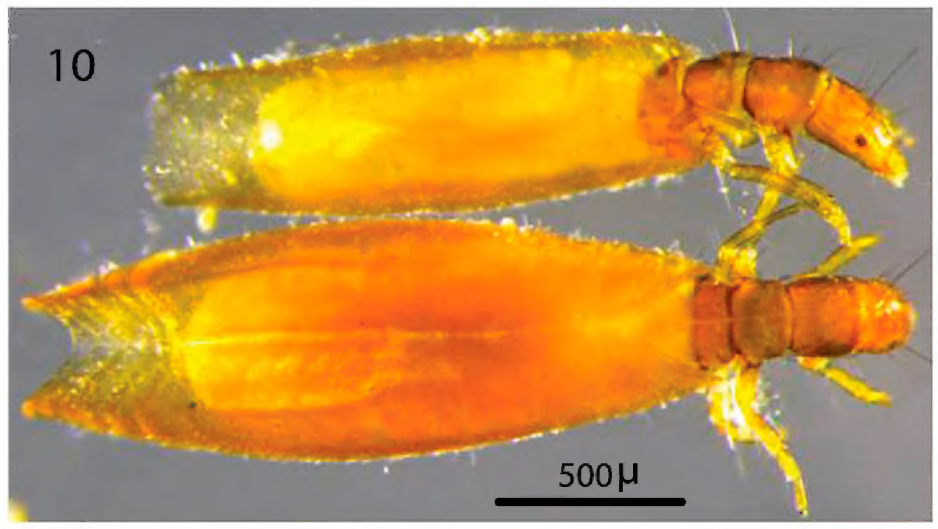
Additional generic features of males include the general form of the phallus which appears to be almost invariant: generally, elongate and straight with a median spiral titillator (Figs 24, 32), the point of origin of which

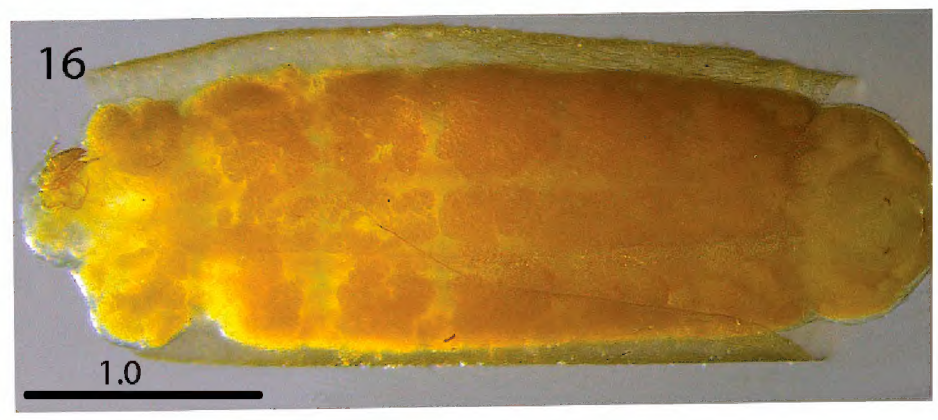


Figures 1–9. Immature stages of typical Australian *Orthotrichia* species; **1.** Larval labrum with characteristic 'tooth'; **2, 3.** *O. bishopi* case, dorsal and lateral; **4.** *O. tortuosa* case, dorsal, arrows indicate; **5, 6.** *O. turrita* case, dorsal and lateral; **7, 8.** *O. bishopi* mature larva, dorsal, lateral; **9.** *Orthotrichia* sp. early instar larva. [After Wells 1979[1980]].

separates a relatively broad proximal part from the unadorned and often very slender, intromittent part (aedeagus) that carries the ejaculatory duct and terminates in a short, slightly expanded, cup-shaped apex. Rarely the phallus is stout distally or slightly twisted or has a tight constriction at one point along its length. Often a single spiny process (generally termed a paramere) is present, associated with the phallus and attached basally to an apodeme that appears to be situated asymmetrically within the abdomen. This spine is usually straight but is sometimes bent, twisted or hooked distally (Fig. 18), even shaped like a corkscrew in one species (Fig. 25).

The inferior appendages are usually symmetrical (Figs 18, 22, 25, 30), sometimes asymmetric (Figs 20, 28, 32), in most species fused at least basally, rarely discrete, and usually strongly reduced such that any kind of



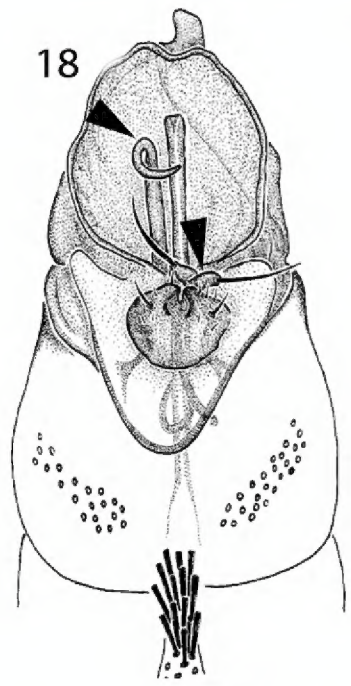


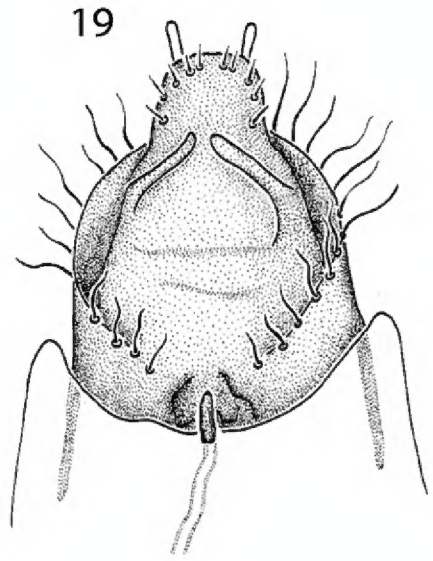
Figures 10–17. Cased immature stages of some Australian *Orthotrichia* species: **10–13.** Early and mature final instar larvae and pupae, illustrating the tight fit of larvae and pupae within their cases. **14–17.** Stages of the parasitoid aberrans group species: **14.** Free-living early final instar larva of *O. aberrans* prior to entrapment in pupal case of host; **15, 16.** Well-advanced final instar larvae of *O. gressitti* taken from pupal case of host and showing grossly swollen abdomen and the transparent case; **17.** Pupa of *O. gressitti* showing tooth on head. [Fig. 15, after Wells 2020].

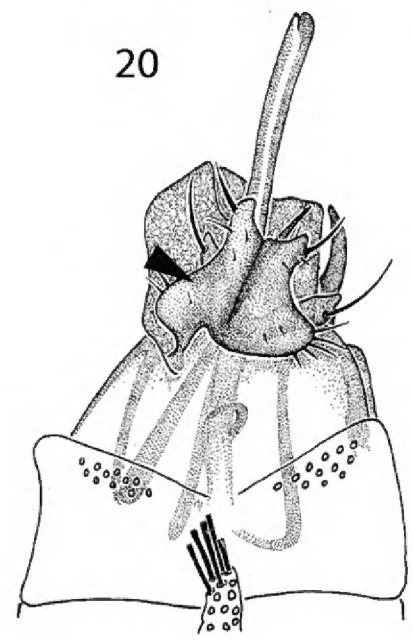
clasping function appears to have been lost. The dorsal bilobed process associated with the inferior appendages, too, may be symmetrical or asymmetrical, usually membranous, sometimes forming a pair of discrete lobes, but again, often fused and sometimes highly modified, usually each lobe tipped by an apical seta (Figs 18, 24). Often the bilobed process is difficult to see and is easily overlooked. Another distinguishing characteristic that is often overlooked, is a slender mid ventral, internal apodeme that arises basally on the unit formed by the inferior appendages and the bilobed process and extends anteriorly in the abdomen (Figs 25, 28, 33).

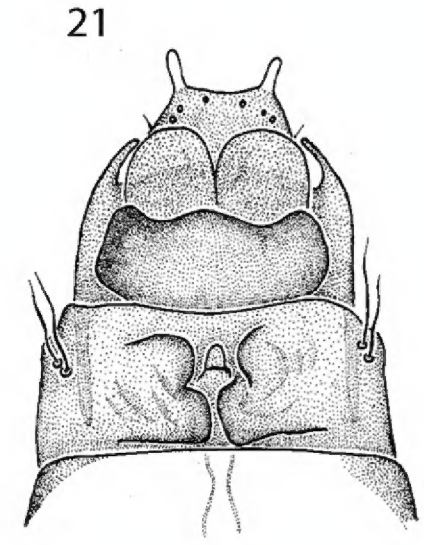
Four species groups were recognised by Marshall (1979) based on the form of the male genitalia. She suggested also that two New Guinean species with very simple genitalia may form another group, which she termed the *kokodana*-group. Wells (1979 [1980]) recognized another group, the *adornata*-group, most species of which may belong in the *kokodana*-group. Two other very distinct species groups can be recognized among Australian *Orthotrichia*. These are what Wells (1979 [1980]) termed the *aberrans*- and *gracilis*-groups. All groups recognized for Australian *Orthotrichia* species also appear to occur in the New Guinean fauna, and the *aberrans* group in Sulawesi, but *aberrans* and *gracilis*-group species have not been recognized in other parts of the world distribution. The two *aberrans*-group species with which immatures (Figs 14–17) have been associated are parasitoids of hydropsychid and philopotamid pupae (Wells 1992, 2005). Adults of all members of this group tend to be relatively large and robust in comparison with other congeners. Adult males recognized as *gracilis*-group members have at least one pair of long, black, generally stout, setae at the apical (distal) margin of abdominal tergite VIII or medially on the tergite (Figs 26, 29, 31, 33).

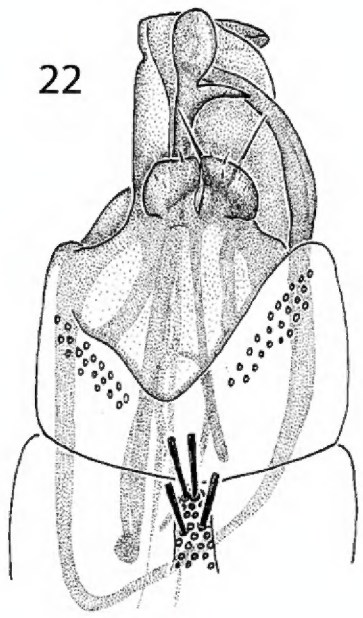
Given that *Orthotrichia* is not known from New Caledonia, New Zealand or south-western Australia, and that the Australian region has these distinctive groups among species of *Orthotrichia*, it is probably safe to assume the founding stock of the lineage or lineages in Australia derived from the Oriental Region. What selective pressures could have led to its high diversity in the Australian

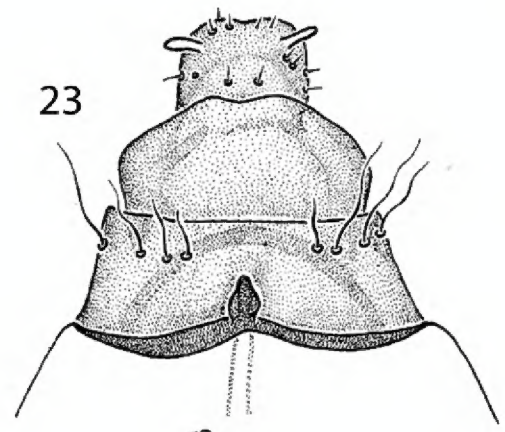


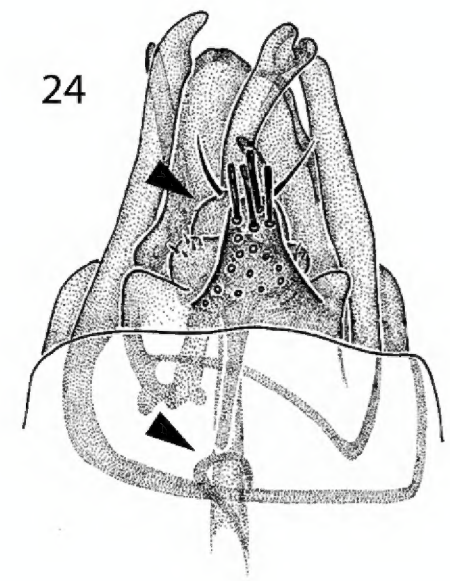


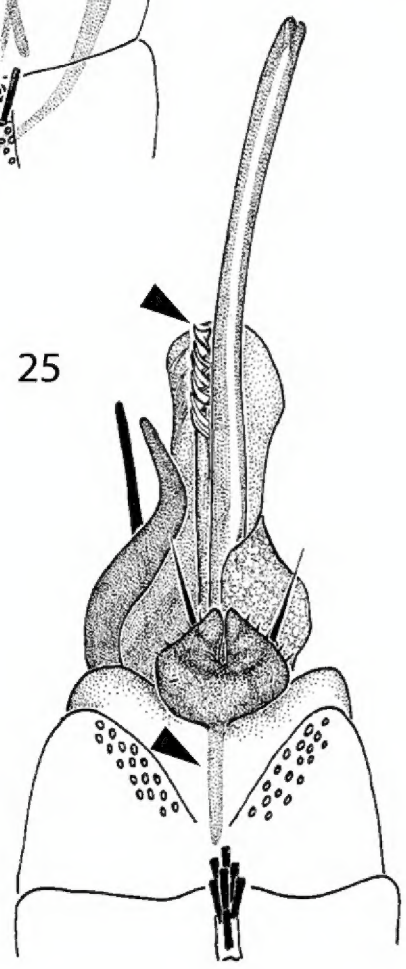


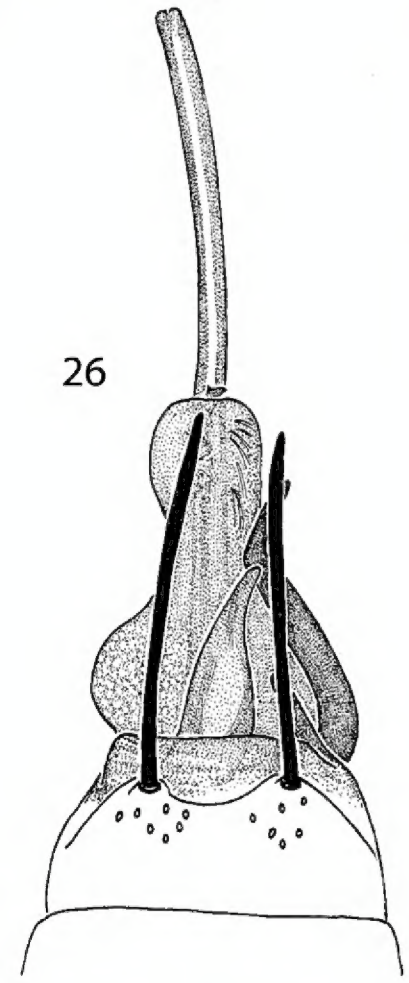


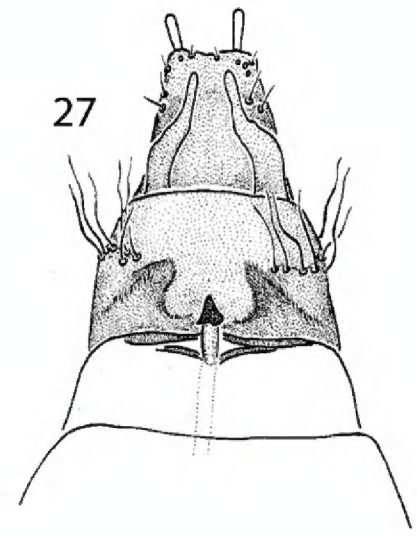










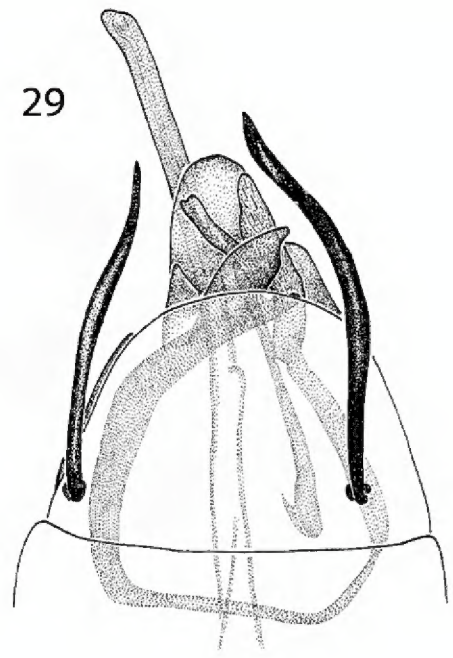


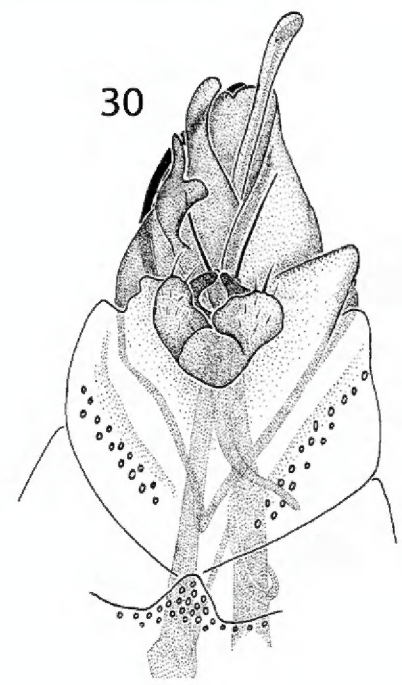
Figures 18–27. Male and female genitalia of typical Australian *Orthotrichia* species; **18, 19.** Ventral views of male and female *O. bishopi*; **20, 21.** Ventral views of *O. morula*; **22, 23.** Ventral views of *O. rostrata*; **24.** Ventral view of *O. aberrans* male; **25–27.** *O. tortuosa* male ventral and dorsal views, female ventral view. [After Wells 1979[1980]].

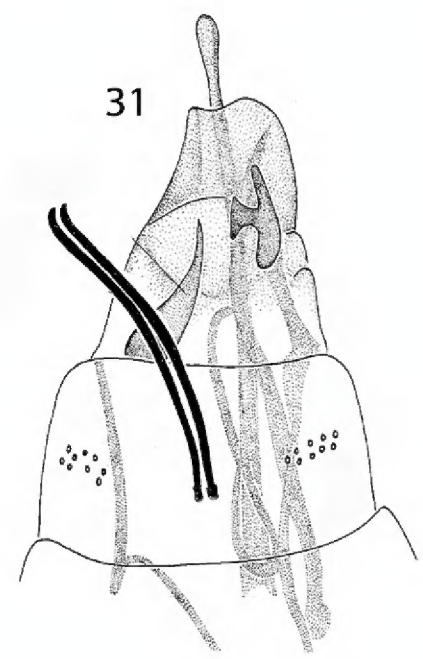
Region? One can assume that whatever the selective pressures are or have been, they might operate at any or all life stages—adult, pupal and/or larval stages.

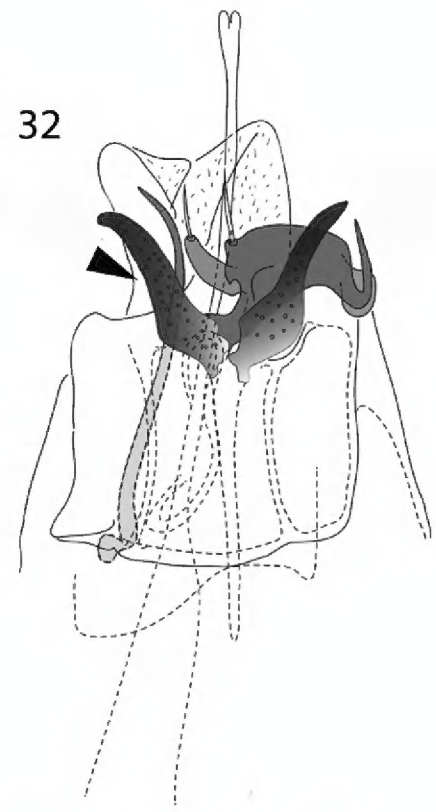
Biology

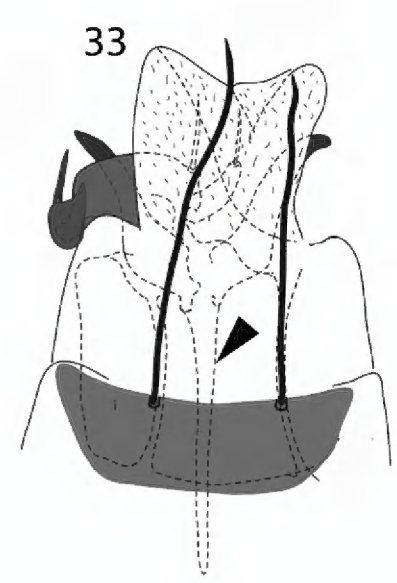
Looking first at the immatures. Nielsen (1948) described more than the morphology of larval *Orthotrichia*. He described in detail the feeding on filamentous green algae by the lentic-dwelling final instar larvae of *O. costalis* [as *O. tetensii*], noting that the larva uses the mandibles to bite into the algal cell and the labral tooth is inserted into the cell to form, with the left mandible, a tube through which the contents of the cell are sucked. (Such a system is analogous to the feeding method of thrips which is effected by insertion of their single mandible into plant cells, followed by a sucking action (Heming 1978)). However, food sources other than filamentous algae have also been reported for *Orthotrichia* larvae.











Figures 28–33. Male genitalia of Australian *Orthotrichia* species, all assigned to the '*gracilis*-group' characterised by stout black dorsal spines, ventral and dorsal views: **28, 29.** *O. tyleri*; **30, 31.** *O. bellicosa*; **32, 33.** *O. pethericki*. [28–31, after Wells 1979[1980]]; 32, 33, after Wells and Dostine 2016].

Burton and McRae (1972) and Disney (1973) reported larvae feeding on *Simulium* (black fly) larvae in Cameroon and Ghana, respectively, and Wells (1985) reported finding fifth instar larvae of *Orthotrichia* species among and apparently feeding on eggs in egg masses of aquatic insects in south-eastern Australia. More recently, Wells' observations were confirmed in an ecological study, again in south-eastern Australia, involving egg predation by larvae of *Orthotrichia armata* (Bovill et al. 2014). These authors made available to larval *O. armata* egg masses of nine different Trichoptera species from two families: Hydrobiosidae and Hydropsychidae. The objective of their project was to test egg mass choice and characteristics and they demonstrated active predation on Trichoptera egg masses by final instar larvae of an *Orthotrichia* species. Also of note is that these larvae prey upon eggs of other caddisflies.

Discussion

Wells (1985) suggested that the toothed labrum of larvae could have pre-adapted them for a shift to feeding on eggs. Was it significant that Nielsen (1948) noted that when offered a choice of algal filaments, *O. costalis* selected the tougher, thicker walled filaments? Has that some significance to a shift from feeding on algal cell contents? Could a radiation of *Orthotrichia* species have been influenced, at least in part, by a switch in feeding habits to a readily available and rich source of larval food? This is pure speculation, but feasible with the incursion of *Orthotrichia* into Australia post-dating a very extensive Australian-Region radiation of the Gondwanan family Hydrobiosidae, many of which produce 'jelly spare' egg masses (Bovill et al. 2014). The other oddity, mentioned above, is the parasitoid habit of the known final instar larvae of the *aberrans*-group (Figs 15, 16; Wells 1992, 2005) also parasitising other caddisflies.

Have adaptive shifts to these specialist predatory larval-feeding niches been responsible for the quite extensive radiation of the genus in the Australian Region or at least been a major contributing factor? Is it significant that tropical Africa is also rich in *Orthotrichia* species, and it is from there that predatory behavior has also been reported?

Larvae of the two Australian species collected from lentic waters have curiously specialized cases, suggesting that their adoption of the lentic niche could be secondary.

These species are found in billabongs in the seasonal monsoon area of the north of Australia and their cases are equipped with a pair of small dorsal vents. Billabongs are anabranchs of rivers and, when temperatures are high towards the end of the wet season and later in the 'build up' season, the waters in these shallow macrophyte-rich lakes are often low in oxygen (Walker et al. 1984). The unusual vents in these cases (Figs 5, 6) presumably aid circulation of water in the case (Wells 1985), and hence obviate the total reliance on diffusion of oxygen across the case wall, probably being especially important in the pupal stage. The case adaptations have probably developed independently in the two species as, based on male genitalia, they are assigned to two separate species groups. (Similar vents are seen in cases of a New Caledonian hydroptilid species, *Caledonotrichia illiesi* Sykora).

However, in the several *aberrans*-group species for which immatures have been associated, the cases and the pupae are distinctive (Figs 15–17): the cases are very flimsy and transparent and the pupae bear varying-sized 'beaks' on the head (Fig. 17). The final cases are protected within the pupal cases of the host and putting less energy into case construction could be adaptive; Wells (1992) suggested that the pupal 'beak' probably assists the pharate adult to break out of the coarse sand-grain pupal case of the host.

While adaptive shifts by larvae could have led at least in part to the radiation of *Orthotrichia* in the Australian Region, as with many hydroptilids, it is the distinctive male genitalia that attract one's notice. Our species discrimination of hydroptilids is based for the main part on features of male genitalia. In the genus *Orthotrichia*, these male structures are often highly complex, and, as noted above, distinguishing features can be recognized among the few associated females.

In contrast to some of the diurnally active Trichoptera species, e.g., some leptocerids (Gullefors and Petersson 1993), the hydropsychid genus *Macrostemon* (Silva and Paprocki 2020) and some hydroptilids (e.g., Wells 2002), no evidence of any pre-mating courtship behavior has been reported or observed (by the author) in *Orthotrichia* species. The complexity of male genitalic structures in *Orthotrichia* species immediately suggests the operation of sexual selection involving a 'lock and key' mechanism. Evidence is accumulating in some non-Trichoptera groups (Ah-King 2014) on the matching complexity of female structures to male. As yet only few Trichoptera studies have associated females and males and certainly, as noted above, very few for *Orthotrichia* species.

Hypotheses of sexual selection involving lock and key mechanisms are not particularly popular (see Simmons 2014). Most recent hypotheses invoke sensory lock and key systems (Masly 2012), rather than purely mechanical systems, since the non-intromittent structures (i.e. the 'secondary genitalic structures' sensu Sloan and Simmons 2019) are the more elaborate parts, and are presumed to require a precise fit.

In males of most species of *Orthotrichia* the inferior appendages are generally so greatly reduced that they appear to be unsuited to perform the more usual clasping function. Perhaps the often berry-like complex formed by the inferior appendages and their dorsal bilobed processes is involved in sensory stimulation of the female, while other structures could hold the male abdomen in place during copulation.

The simple almost invariant form of the intromittent organ (Figs 18, 20, 25, 28, 30, 32) contrasts with the phallus of many other hydroptilid genera, in which the phallus is often equipped with hooks or spines. Such structures have been demonstrated in some non-Trichoptera groups to play a role in displacement of rival sperm from the female tract (Córdoba-Aguilar and Cordera Riviera 2006). However, in *Orthotrichia* species, the 'paramere' could play a similar role and the cup-shaped apex could also function in spermatophore removal as postulated in an anisolabidid earwig by Kamimura (2000).

Instability among genes controlling development of male genitalic structures, leading to sensory or mechanical modifications and consequent incompatibility, thence reproductive isolation, could explain, again at least in part, the radiation of the genus (Wojcieszek and Simmons 2013).

So much of this is speculative. I hope it provides a stimulus for others to explore the life histories, distributions, morphological adaptations, and behavior of Trichoptera.

References

Ah-King M, Barron AB, Herberstein ME (2014) Genital Evolution: Why are females still understudied? PLoS Biology12(5): e1001851. https://doi.org/10.1371/journal.pbio.1001851

Bovill WD, Downes BJ, Lancaster J (2014) Caddisfly egg mass morphology mediates egg predation: potential costs to individuals and populations. Freshwater Biology 60: 360–372. https://doi.org/10.1111/fwb.12497

Burton GJ, McRae TM (1972) Observations on trichopteran predators on aquatic stages of *Simulium damnosum* and other *Simulium* spp. in Ghana. Journal of Medical Entomology 9: 289–294. https://doi.org/10.1093/jmedent/9.4.289

Cartwright D, Wells A, Dean J, St Clair R, Shackleton M (2013) Taxonomic status and distribution of Australian caddisflies (Insecta: Trichoptera). Aquatic macroinvertebrates 2013 Taxonomic Workshop, La Trobe University, Albury-Wodonga.

Córdoba-Aguilar A, Uhia E, Cordero Rivera A (2006) Sperm competition in Odonata (Insecta): the evolution of female sperm storage and rivals' sperm displacement. Journal of Zoology 261(4): 381–398. https://doi.org/10.1017/S0952836903004357

Disney RHL (1973) Larval Hydroptilidae (Trichoptera) that prey upon Simuliidae in Cameroon. Entomologist's Monthly Magazine 108(1972): 84–85.

Gullefors B, Petersson E (1993) Sexual dimorphism in relation to swarming and pair formation patterns in leptocerid caddisflies (Trichoptera: Leptoceridae). Journal of Insect Behavior 6: 563–577. https://doi.org/10.1007/BF01048123

Harris S, Davenport LJ (1999) New species of Hydroptilidae (Trichoptera) from the Amazon region of northeastern Peru. Proceedings-Entomological Society of Washington 101(1): 26–38.

Harris SC, Rasmussen AK (2019) Review of the *Orthotrichia* (Trichoptera: Hydroptilidae) of Florida, with descriptions of previously unknown females of three species. Zoosymposia 14: 215–230. https://doi.org/10.11646/zoosymposia.14.1.24

Heming BS (1978) Structure and function of the mouthparts in larvae of *Haplothrips verbasci* (Osborn) (Thysanoptera, Tubulifera, Phlaeothripidae). Journal of Morphology 156(1): 1–37. https://doi.org/10.1002/jmor.1051560102

Kamimura Y (2000) Possible removal of rival sperm by the elongated genitalia of the earwig, *Euborellia plebeja*. Zoological Science 17: 667–672. https://doi.org/10.2108/zsj.17.667

Marshall JE (1979) A review of the genera of the Hydroptilidae (Trichoptera). Bulletin of the British Museum (Nat. Hist.) Entomology 39: 135–239.

Masly JP (2012) 170 Years of "Lock-and-Key": Genital Morphology and Reproductive Isolation. International Journal of Evolutionary Biology 2012: [Article ID] 247352. [10 pp] https://doi.org/10.1155/2012/247352

Morse JC [Ed.] (2022) Trichoptera World Check List. http://www.clemson.edu/cafls/departments/esps/database/trichopt/index.htm [original version effective 27 March 1999] [Accessed Sept. 2022]

Nielsen A (1948) Postembryonic development and biology of the Hydroptilidae. Biologiske Skrifter 4(1): 1–200.

Ross HH (1944) The caddis flies, or Trichoptera, of Illinois. Bulletin of the Illinois State Natural History Survey 23: 1–326. https://doi.org/10.21900/j.inhs.v23.199

Silva LM, Paprock H (2020) Description of female genitalia, additional morphological variations, and courtship behavior and copulation of *Macrostemum brasiliense* (Fischer 1970) (Trichoptera: Hydropsychidae). Zootaxa 4858(3): 438–446. https://doi.org/10.11646/zootaxa.4858.3.9

Simmons LW (2014) Sexual selection and genital evolution. Austral Entomology 53: 1–17. https://doi.org/10.1111/aen.12053

Sloan NS, Simmons LW (2019) The evolution of female genitalia. Journal of Evolutionary Biology 32: 882–899. https://doi.org/10.1111/jeb.13503

Walker TD, Waterhouse J, Tyler PA (1984) Open File Record 28. Thermal Stratification and the Distribution of Dissolved Oxygen in Billabongs of the Alligator Rivers Region, Northern Territory. (Final report) Prepared by Department of Botany, University of Tasmania, Hobart September 1984 Supervising Scientist for the Alligator Rivers Region. A Limnological Survey of the Alligator Rivers Region. Northern Territory. 2. Thermal stratification and the distribution of dissolved oxygen in the billabongs. https://www.dcceew.gov.au/sites/default/files/documents/ofr028.pdf

Wells A (1979[1980]) The Australian species of *Orthotrichia* Eaton (Trichoptera: Hydroptilidae). Australian Journal of Zoology 27: 585–622. https://doi.org/10.1071/ZO9790585

Wells A (1984) Comparative studies of antennal features of adult Hydroptilidae (Trichoptera), 423–440. In: Morse JC (Ed.) Proceedings of the 4th International Symposium on Trichoptera. The Hague, Dr. W. Junk.

Wells A (1985) Larvae and pupae of Australian Hydroptilidae (Trichoptera), with observations on general biology and relationships. Australian Journal of Zoology Supplement 113: 1–69. https://doi.org/10.1071/AJZS113

Wells A (1991) A guide to the caddisflies (Trichoptera) of the Alligator Rivers Region, Northern Territory. Open File Record 84, Supervising Scientist for the Alligator Rivers Region, 105 pp.

Wells A (1992) The first parasitic Trichoptera. Ecological Entomology 17: 299–302. https://doi.org/10.1111/j.1365-2311.1992.tb01061.x

Wells A (2002) Three new species of *Orphninotrichia* Mosely (Trichoptera: Hydroptilidae) from Barrington Tops, New South Wales, a distribution extended, and remarks on generic placement. Australian Journal of Entomology 41: 221–225. https://doi.org/10.1046/j.1440-6055.2002.00295.x

Wells A (2005) Parasitism by hydroptilid caddisflies (Trichoptera) and seven new species of Hydroptilidae from northern Queensland. Australian Journal of Entomology 44: 385–391. https://doi.org/10.1111/j.1440-6055.2005.00492.x

Wells A, Dostine P (2016) New and newly recorded micro-caddisfly species (Insecta: Trichoptera: Hydroptilidae) from Australia's north, including islands of Torres Strait. Zootaxa 4127(3): 591–600. https://doi.org/10.11646/zootaxa.4127.3.11

Wells A (2020) Curious Caddis Couture: Form and function among cases of Australian. Zoosymposia 18: 24–33. https://doi.org/10.11646/zoosymposia.18.1.6

Wells A, De Moor FC (2020) Hydroptilidae (Trichoptera) of Angola, a new genus, seven new species, and five new records. Zootaxa 4868(4): 495–514. https://doi.org/10.11646/zootaxa.4868.4.2

Wells A, Johanson KA (2016) Micro-caddisfly faunas of Australia and the southwest Pacific (Trichoptera, Hydroptilidae). Zoosymposia 10: 439–450. https://doi.org/10.11646/zoosymposia.10.1.41

Wiggins GB (1977) Larvae of the North American Caddisfly Genera (Trichoptera). 1st Edn. University of Toronto Press: Toronto, Ontario, Canada.

Wiggins GB (2004) Caddisflies: The Underwater Architects. University of Toronto Press. https://doi.org/10.3138/9781442623590

Wojcieszek JM, Simmons LW (2013) Divergence in genital morphology may contribute to mechanical reproductive isolation in a millipede. Ecology and Evolution 3(2): 334–343. https://doi.org/10.1002/ece3.466